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Source: American Museum Novitates, 2005(3475) : 1-20

Published By: American Museum of Natural History

URL: [https://doi.org/10.1206/0003-0082\(2005\)475\[0001:ANSSFT\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2005)475[0001:ANSSFT]2.0.CO;2)

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AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3475, 20 pp., 5 figures, 1 table

May 11, 2005

A New Spalacotheriid Symmetrodont from the Early Cretaceous of Northeastern China

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ABSTRACT

Symmetrodonts are Mesozoic mammals having lower molars with nearly symmetrical trigonids but lacking talonids. They appear to be stem members of the mammalian clade that led to extant tribosphenic mammals, but the fossil record of symmetrodonts is poor. Here we report a new genus and species of an acute-angled spalacotheriid symmetrodont, *Heishanlestes changi*, n.gen. and n.sp., represented by well-preserved lower jaws with teeth from the Early Cretaceous of northeastern China. The new mammal has four tightly spaced premolars and three morphological groups of lower molars, in which the first molar has an obtuse trigonid angle and the last two molars have a large neomorphic cusp in the center of the trigonid, a feature not seen in other mammals. *Heishanlestes* appears to be a specialized member of the spalacotheriid subfamily, Spalacolestinae, which is otherwise only known from North America. The animal probably used the premolars to crush its prey before shearing it with the molars.

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INTRODUCTION

Symmetrodonts are Mesozoic mammals having three principal cusps on upper and lower molars arranged in a reversed triangle pattern (Cifelli and Madsen, 1999). The first known symmetrodont mammal, *Spalacotherium*, was described by Richard Owen in 1854. Two other symmetrodont genera, *Tinodon* and *Peralestes*, were also found in the 19th century (see Simpson, 1925a, 1928, 1929) and were first regarded as specialized triconodonts (see Simpson, 1925a, 1925b, 1928; Cassiliano and Clemens, 1979). Simpson (1925a) recognized the unique significance of the symmetrodont molar pattern in the evolution of the mammalian dentition and accordingly established the order Symmetrodonta, including two families, Amphidontidae and Spalacotheriidae (Simpson, 1925b). Crompton and Jenkins (1968) added the family Kuehneotheriidae Kermack, Kermack & Mussett, 1968, to Symmetrodonta based on the occlusal pattern shared between *Kuehneotherium* and symmetrodonts. Most students have accepted this assignment (Casiliano and Clemens, 1979; Datta, 1981; Yadagiri, 1984; Fox, 1985; Kielan-Jaworowska, 1992; Sigogneau-Russell and Ensom, 1998; Ensom and Sigogneau-Russell, 2000; Averianov, 2002), but a few excluded Kuehneotheriidae from the order based on results of phylogenetic analyses (McKenna, 1975; Prothero, 1981; McKenna and Bell, 1997). In total, about 30 genera of Mesozoic mammals have been assigned to the order at one time or another, but more than half of these genera have since been found to be closer to other mammals than to symmetrodonts (see McKenna and Bell, 1997, and Averianov, 2002, for latest versions of cladistic and noncladistic classification, respectively), while some others are now regarded as junior synonyms or *nomina dubia*.

Most symmetrodonts are represented by isolated teeth or jaw fragments with teeth. Only two genera, *Zhangheotherium* and *Maotherium*, both from the Jehol paleobiota of northeastern China (Hu et al., 1997, 1998; Ji, 2002; Rougier et al., 2003) have the complete skeleton preserved, but the dentitions of even these specimens are only partially

exposed and available for study. *Spalacotherium*, from the Purbeck beds of England, is represented by several upper and lower jaws with teeth (Owen, 1854; Simpson, 1928; Clemens, 1963a, 1963b; Ensom and Sigogneau-Russell, 2000), but this material has suffered damage and much of the detail of the dentition is no longer visible (Clemens, 1963b; Parrington, 1973). Numerous specimens of spalacotheriid symmetrodonts have been recovered from the Cretaceous of Utah (Cifelli and Madsen, 1999, and references therein). The majority of these specimens are isolated teeth, a few are fragmentary lower jaws with teeth, and only one specimen, which has yet to be described (Cifelli et al., 2000), preserves all of the cheek teeth in situ. Symmetrodonts have been accorded an important position in the evolution toward tribosphenic mammals (Cifelli and Madsen, 1999), but their poor preservation has hampered the study of their morphology, function, and phylogeny. Here we describe a new genus and species of spalacotheriid symmetrodont from the Early Cretaceous of northeastern China, with the lower jaw and all of the lower cheek teeth well preserved. This new material will help clarify morphological details of the mandible and lower dentition of spalacotheriids, and adds new evidence toward clarifying the position of symmetrodonts in mammalian phylogeny.

MATERIALS AND METHODS

During the field seasons of 1994–1995 three specimens of symmetrodonts were collected from coal-bearing sediments in three small coal mines in Badaohao Town, Heishan County, Liaoning Province, China (Wang et al., 1995). The fossil-bearing layers are associated with the coal seams of the Shahai Formation, which consists of variegated conglomerates, coal measures, and grayish black and green shales. Other mammals collected from the same coal mines include triconodonts, multituberculates, an aegialodontid cladotherid, and eutherians (Wang et al., 1995, 2001). The formation has also yielded the remains of bivalves, gastropods, ostracods, conchostracans, fishes, lizards, and dinosaurs (teeth and egg shells). It over-

lies the Jufotang Formation, which preserves components of Jehol paleobiota. The estimated age of the Shahai Formation is Aptian (Early Cretaceous) (Wang et al., 2001).

All specimens were collected in the field by splitting the fossiliferous matrix with hammers and chisels, and they were further prepared in the laboratory using steel needles under the binocular microscope (Drescher, 2000; Krebs, 2000). Stereoscopic photographs of the specimens were taken using a RT SPOT digital camera mounted on a Nikon SMZ-U stereo-microscope. The SEM images were taken at 2.0 kV with specimens uncoated. All images were further processed using Adobe Photoshop software, Version 6.0.1, on a MacIntosh computer. Linear measurements (table 1) were taken with a Microcode II digital measuring microscope. Angles of teeth were measured in crown view images using the Measure Tool in Adobe Photoshop.

The definition of Mammalia adopted by Luo et al. (2002: 5) is followed in this paper: The Mammalia include the last “common ancestor of *Sinoconodon*, living monotremes, and living therians, plus all its descendants.” Symmetrodonta in this paper is regarded as an order of Mesozoic mammals with molars characterized by an imperfectly symmetrical, triangular arrangement of three principal cusps and without talonid on lower teeth (Simpson, 1925a, 1925b; Cassiliano and Clemens, 1979). We use the terms “pre-molar” and “molar” for the postcanine teeth in the new symmetrodont based on the crown morphology of these teeth and that in other symmetrodonts, but we have no information about their replacement pattern. Abbreviations for lower teeth are: ci, canine; p1, p2, p3, p4, first to fourth premolars; m1, m2, m3, m4, m5, m6, first to sixth molars. Molar terminology follows that of Cifelli and Madsen (1999).

Institutional abbreviations: IVPP, Institute for Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; UALVP, Laboratory for Vertebrate Paleontology, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.

TABLE 1
Measurements of *Heishanlestes changi* (in mm)

	Length	Width	Height (lingual)	Height (labial)
IVPP V 7480				
p1	N	0.77	—	—
p2	0.80	0.75	0.52	0.58
p3	0.73	0.76	0.64	0.71
p4	1.48	0.96	0.83	1.01
m1	1.62	1.13	0.86	1.22
m2	1.21	1.33	0.76	1.42
m3	1.15	1.32	0.84	1.71
m4	1.15	1.30	0.72	1.63
m5	1.01	1.09	0.58	0.97
m6	0.85	0.89	0.56	0.69
Lower jaw				
Length (presevered portion)			17.37	
Height below p4			1.54	1.37
Height below m3			2.31	1.67
Height below m6			2.70	2.13
Coronoid process			3.48 (height)	3.25 (length)
Condyle			1.63 (width)	0.73 (length)
IVPP V 7481				
ci	0.71 ^a	0.58	—	—
p1	0.92 ^a	0.78	0.67	0.69
p2	0.91	0.76	0.80	0.79
p3	0.92	0.75	0.78	0.81
p4	1.58	1.02	0.87	1.20
m1	1.69	1.32	0.84	1.59
Lower jaw height below p4			1.67	1.53
IVPP V 7482				
p4	1.59	0.97	0.92	1.06
m1	1.75	1.10	0.93	1.18
Lower jaw height below p4			1.72	1.66

^a Length of visible part.

SYSTEMATIC PALEONTOLOGY

CLASS MAMMALIA LINNAEUS, 1758

ORDER SYMMETRODONTA SIMPSON, 1925

FAMILY SPALACOTHERIIDAE MARSH, 1887

SUBFAMILY SPALACOLESTINAE CIFELLI AND MADSEN, 1999

Heishanlestes, new genus

TYPE SPECIES: *Heishanlestes changi*, n.sp.

DIAGNOSIS: As for the type and only species.

ETYMOLOGY: “Heishan” is the name of the county in northeastern China in which the materials of the type species were collected.

DISTRIBUTION AND AGE: As for the type and only species.

Heishanlestes changi, new species

Figures 1–5, table 1

HOLOTYPE: IVPP V 7480, a nearly complete right dentary containing p1–4, m1–6 (figs. 1, 3, 4, 5).

REFERRED SPECIMENS: IVPP V 7481, anterior part of a left dentary containing an erupting canine, p1–4, m1 (figs. 2, 3); IVPP V 7482, anterior part of a left dentary containing p4, m1, and alveolus for p3 (fig. 2).

ETYMOLOGY: “changi” is for Professor Zhenglu Chang, from Liaoning Technical University, for his important contribution to the study of Mesozoic stratigraphy and paleontology of northeastern China during the past 50 years.

DIAGNOSIS: Dental formula: ci, p1–4, m1–6, differing from *Spalacotherium tricuspiciens* and *Spalacolestes cretulablatta*, which have seven lower molars; premolars tightly spaced and overlapping; m1 with obtuse trigonid angle; m5–6 reduced in size and with a subcylindrical cusp arising from the center of the trigonid; differing from *Zhangheotherium* and *Maotherium* in having a strong pterygoid crest but absence of an enlarged first incisor, absence of a Meckelian groove, and reduction of cingular cusps on lower molars.

LOCALITY: Badaohao, Heishan County, Liaoning Province, China (coordinates: 41°50'N and 121°55'E).

GEOLOGIC OCCURRENCE: Shahai Formation.

AGE: Aptian, Early Cretaceous.

DESCRIPTION

The holotype (V 7480) preserves all of the cheek teeth, V 7481 contains four premolars and m1, and V 7482 contains p4, m1; thus, the teeth in each of the referred specimens can be compared directly with their counterparts in the other specimens. Except for slight differences in size, wear, and minor postmortem damage, teeth at corresponding loci in these specimens are virtually identical in morphology; hence, we are confident in concluding that the three specimens are conspecific.

LOWER INCISORS: The anteriormost part of

the dentary is missing from all specimens and no direct evidence of the lower incisors remains (figs. 1–3). Nevertheless, the missing part is a small portion of the dentary judged by the shape of the mandibular symphysis, and no enlarged alveoli for incisors are visible. It can be postulated that lower incisors, if present, were small teeth; this condition is also seen in *Spalacotherium*, but differing from *Zhangheotherium*, in which the first lower incisor is enlarged.

LOWER CANINE: V 7481 displays the crown of a tooth that at death was just beginning to emerge from the anterior end of the dentary as preserved; the tooth is anteroventrally adjacent to the first premolar (figs. 2, 3; c1). The crown is robust, unicuspid, broadly lanceolate, and bilaterally compressed. In cross section, its labial side is convex, while its lingual side is marked by two grooves, one adjacent and parallel to the anterior edge of the crown, the other in a comparable position posteriorly; between the grooves, the lingual side of the tooth is swollen. The crown curves somewhat posteromedially toward its tip, which is asymmetrical in labial or lingual view, having a slightly longer anterior than posterior side. The enamel at the tip is chipped, an artifact of preservation.

The unicuspid, lanceolate morphology of this tooth suggests that it is the lower canine (c1), even though much of the tooth crown is still hidden within the dentary, out of view, and its height cannot be determined. At its mouth, the alveolus for this tooth is much larger than the visible parts of the tooth (fig. 3A), suggesting that in *Heishanlestes changi* there was a deciduous predecessor at this locus. Whether the lower canine had one or two roots is unknown. The anterior end of the holotype dentary is damaged at the canine position and provides no additional information about the tooth. The lower canine in spalacotheriids is otherwise known only in *Spalacotherium tricuspiciens*, in which it is two-rooted (Simpson, 1928), and *Zhangheotherium* and *Maotherium*, in which it is single-rooted (Hu et al., 1998; Ji 2002; Rougier et al., 2003).

LOWER PREMOLARS: There are four lower premolars in *Heishanlestes changi* (figs. 1–3). As shown in the holotype and V 7481, these are spaced unusually closely to one an-

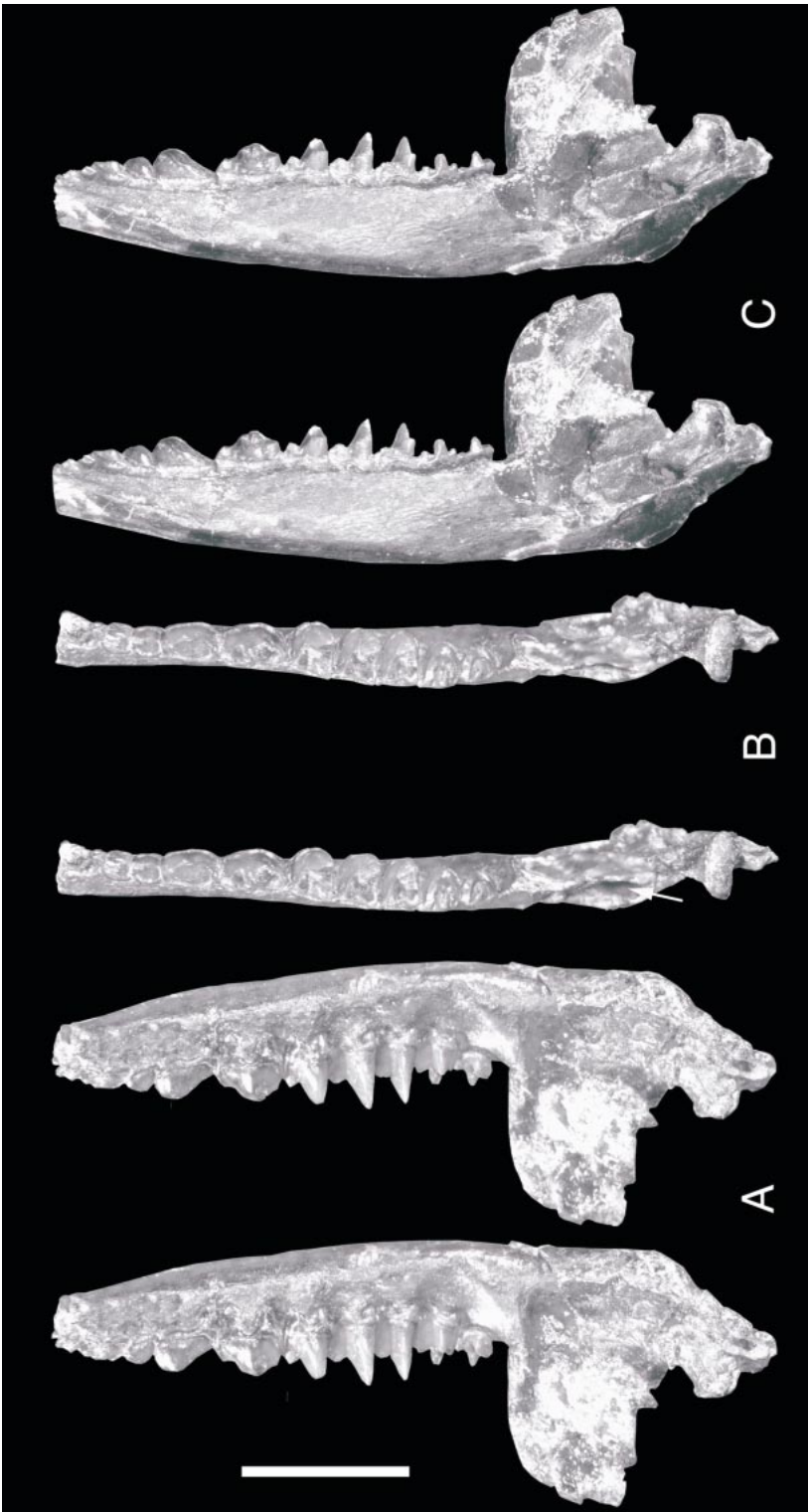


Fig. 1. Stereoscopic views of the right dentary and cheek teeth of *Heishanlestes changi* (IVPP V 7480, holotype). **A**, lateral view; **B**, crown view; **C**, medial view. Arrow in **B** indicates the pocket behind the pterygoid crest. Scale bar is 5 mm.

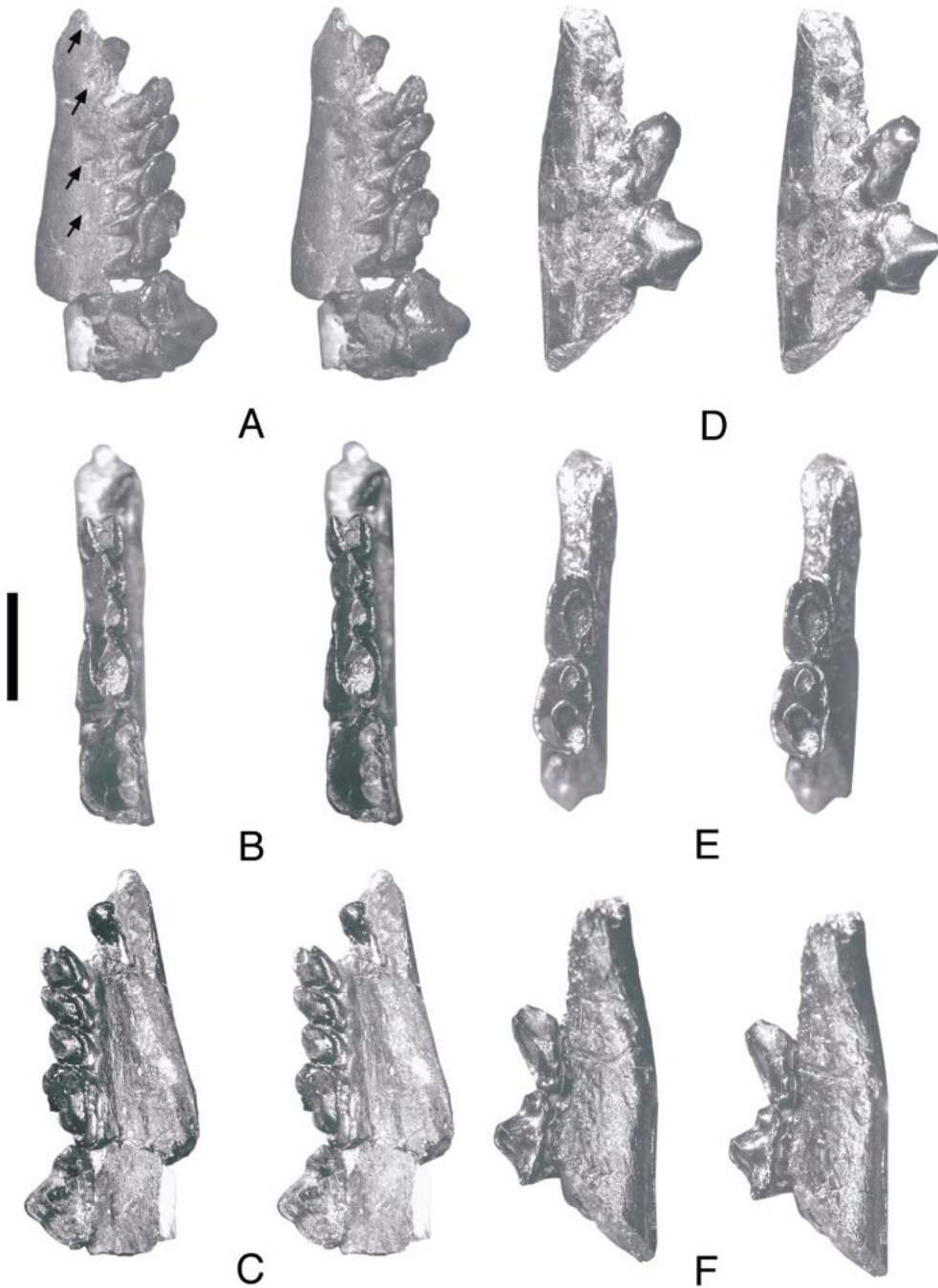


Fig. 2. Stereoscopic views of anterior parts of the left dentaries and anterior cheek teeth of *Heishanlestes changi*. **A**, lateral; **B**, crown; and **C**, medial views of IVPP V 7481 (with c1–m1). **D**, lateral; **E**, crown; and **F**, medial views of IVPP V 7482 (with p4 and m1). Arrows in **A** indicate mental foramina. Scale bar is 2 mm.

other along the tooth row, with the anterior parts of the crown projecting forwards, to overlap substantially on to the posterior parts of the preceding premolar. The result is a unique, tightly imbricated pattern of tooth crowns along the row, from p1 to p4. Whether this pattern extended further forward, with p1 overlapping on to the base of the canine, perhaps meeting a small heel there, cannot be determined directly because of the incompletely erupted canine in V 7481. Although p1 of this specimen is damaged anteriorly (only an uninformative remnant of the crown of p1 is present in the holotype), enough remains to suggest that there may indeed have been a contact similar to that between the premolars, with the anterior part of p1 overlapping the posterior side of the canine at its base. At the other end of the premolar series, the first lower molar (m1) overlaps only on to the posterior basal cingulid of the fourth premolar. This is best shown in the holotype and V 7482 (figs. 2, 3), m1 in V 7481 having been somewhat displaced relative to p4. Each of the premolars shows an ovate worn area on the posterolingual side of the main cusp, beginning at its apex and exposing the dentine. The areas are shallowly to deeply concave, suggesting a crushing action with the crowns of the upper premolars, rather than a vertical shear between teeth.

The fourth lower premolar is the largest of the premolar series, followed by p1 and then p2 and p3, which are subequal in size and appear to be slightly smaller than p1. Owing to damage, the dimensions of p1 cannot be determined in the holotype. In V 7481 the anteriormost parts of the crown of p1 have been broken away and lost (figs. 2, 3). In this specimen, however, enough of the tooth remains to show that p1 is slightly wider than p2 or p3 and like them, was ovate in occlusal outline, being wider posteriorly than anteriorly; the lingual side of the remnant of the crown is more swollen than labially. A robust cingulid is developed labially and lingually, but whether it was continuous across the anterior side of the crown cannot be determined owing to the breakage that the tooth has sustained. If the cingulid is present posteriorly, it is concealed by the overlap of p2. Only a single root is visible at the mouth of the p1 alveolus, although it may divide into two

more deeply in the dentary. What remains of the anteroventral surface of p1 is concave, forming a broad inverted "V", strongly suggesting articulation with the adjacent posterior surface of the canine as noted above.

The second lower premolar is somewhat damaged both in the holotype and V 7481. It has a single principal cusp. In occlusal view, the crown is ovate, being slightly wider posteriorly than anteriorly. In side view, its base rises steeply and projects anteriorly, jutting out well beyond the root beneath. The principal cusp is low, somewhat compressed bilaterally, and more swollen on its lingual side than labially. A short crest that curves slightly labially runs down the posterior side of the cusp, from its apex. The anterior face of p2 is concave and fits over the postero-dorsal surface of p1, forming a specialized, broad interlock between the two teeth. On both sides of the crown the cingulid is deepest posteriorly. It fails to cross the concave surface that meets p1. Whether the cingulid is developed across the posterior edge of the crown cannot be determined owing to the overlap of p3. The two roots of p2 are clearly visible in V 7481. They appear subequal in cross dimensions, with the anterior root nearly vertical and the posterior root diverging posteroventrally from it as they enter the dentary.

The third lower premolar is well preserved in the holotype and V 7481. It closely resembles p2 in size and morphology. A short anterior crest, the summit of which is worn, descends from the apex of the principal cusp to the articulation surface with p2. Like p2, p3 is two-rooted. Both roots slant somewhat obliquely posteriorly, with the posterior root descending at the more oblique angle.

The fourth lower premolar is substantially larger than the more anterior premolars, but otherwise closely resembles them in coronal features. Its crown rises anteriorly and overlaps p3. The exposed anteroventral base of the crown of p4 in V 7482 is deeply cleft posteriorly to the base of the anterior root for the overlap with p3. The principal cusp is very large and appears to have been the only cusp on the crown, but much of its original surface is worn posterolingually in each of the three specimens, from apex to base. Any cusplule or other structure originally in this

area would have been abraded away during life. The anterior crest that descends from the principal cusp is slightly longer than on p3. Just labial to this crest in the holotype, a small wear facet can be seen high on the anterolabial face of the cusp (indicated by arrow in fig. 3D). The basal cingulid is robust labially and lingually. It is relatively deep anteriorly, at the level of the anterior root, but becomes somewhat shallower between the roots where it is dorsally flexed, more so labially than lingually. It then deepens again, especially on the labial side, and crosses the posterior edge of the crown, where it is deepest. There it rises into a low point (best seen in the holotype) at the junction between the labial and lingual limbs of the cingulid, just lingual to the midwidth of the crown. The posterolabial limb of the basal cingulid is deeply worn on V 7481, extending from the posteriormost parts of the posterolingual wear facet to the labial border of the crown (arrow in fig. 3A). The facet probably resulted from shearing with upper teeth. It, together with worn area on the principal cusp, implies a more complex occlusal function with the upper dentition than that affecting p1–3. There are two roots, each slanting obliquely posteriorly (the posterior root more strongly so) as they enter their alveoli.

LOWER MOLARS: The holotype preserves the full complement of six lower molars, but only m1 of V 7481 and V 7482 is preserved (figs. 1–4). All molars are two-rooted, as in other symmetrodonts. Morphologically, the molars are unusually heterodont for a symmetrodont and can be readily separated into three groups according to differences in their coronal structure. If found as isolated specimens, teeth from each group would likely be identified as pertaining at least to separate genera. The m1 is distinct from the other molars in that its trigonid forms a broadly obtuse angle (about 140°), and the paraconid and metaconid are only slightly more lingual than the protoconid. The second, third, and fourth molars are closely similar to each other and differ substantially from m1; in them, the trigonid angle is acute, as in “acute-angled” symmetrodonts, with the angle in m2 being slightly more obtuse than that in m3 and m4, in which the angle is subequal (m2: 55°, m3: 48°, m4: 46°). The crowns are much

higher labially than lingually (table 1), a character also seen in other spalacotheriids (Cifelli and Madsen, 1999). In m5 and m6, the trigonid angle is more obtuse than that of m4, and m6 (60°) more than m5 (50°), but these teeth differ most from m1–4 in their possession of a robust cusp (* in fig. 4A) lingually positioned on the biting surface of the trigonid. A comparable structure has not been seen before in Mesozoic mammals.

In the holotype and V 7482, m1 is undamaged but in V 7481, its posterolingual basal corner has been broken away; m1 in all three specimens is moderately worn. In occlusal outline, the crown approximates an asymmetrical triangle that is longer anteroposteriorly than wide: The lingual side is the longest and oriented anteroposteriorly; the anterolabial side is longer than the posterolabial side and relative to the long axis of the tooth, is oriented at an angle about 15° compared to 25° for the posterolabial side. The protoconid is the tallest cusp, is located posterior to the midlength of the crown, and its base occupies nearly the entire coronal width between the basal cingulids. The paraconid is the lowest cusp. Although its apex is worn in each specimen, it clearly was slightly lingual to that of the protoconid originally. The metaconid is taller than the paraconid and somewhat larger at its base and is slightly more lingual than latter. The protocristid is substantially higher than the paracristid, and was probably so originally, before wear. A robust and dorsoventrally deep basal cingulid encircles most of the crown. Anteriorly this cingulid is interrupted by a notch at the base of the paraconid for articulation with the posterior end of p4, while posterolingually it projects and abuts upon the anterior end of m2 (arrow in fig. 4B). The projection, the distal cingular cusp in Cifelli and Madsen’s (1999) terminology, is overlapped by the mesial cingular cusp of m2. Labially, the cingulid is inflected dorsally between the two roots. The roots are stout and, as exposed labially in V 7481, are essentially vertical in their orientation; the posterior root is the larger in cross dimensions.

Two patterns of wear are evident on m1. The first, as seen in the holotype, is represented by a continuous, planar, straplike facet that begins at the apex of the paraconid, has

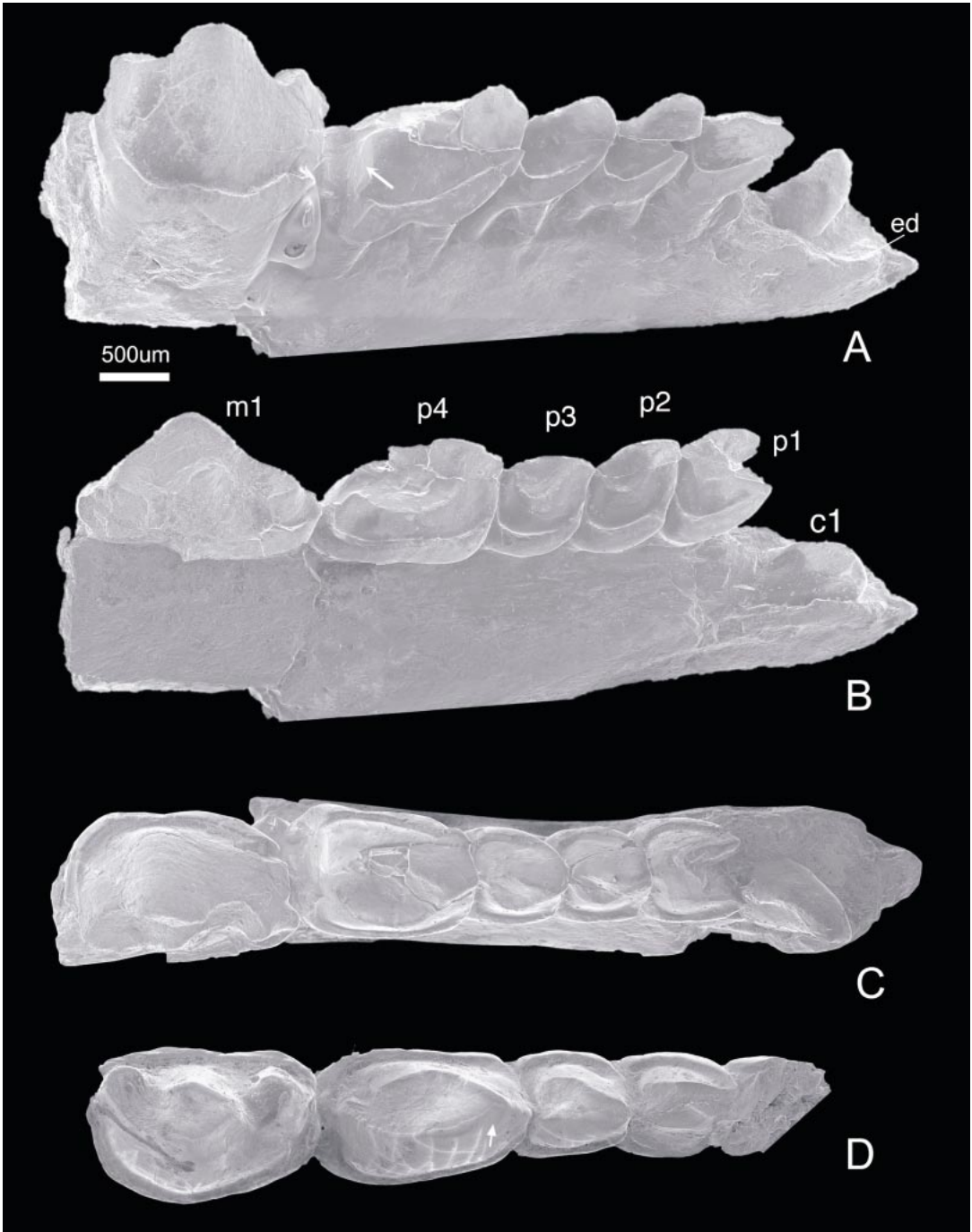


Fig. 3. SEM images of dentaries and anterior cheek teeth of *Heishanlestes changi* (from casts). **A**, laterodorsal; **B**, mediodorsal; and **C**, crown views of IVPP V 7481. **D**, crown view of ci and m1 of IVPP V 7480. Scale bar is for A–D. c1, canine; ed, edge of canine alveolus; m1, first molar; p1–p4, premolars; arrows in **A** and **D** indicate wear facet.

truncated the paracristid, expands over the apex of the protoconid, which has been worn flat, continues along the protocristid, and truncates the apex of the metaconid (fig. 4B). In V 7481, the same basic pattern has been followed, but wear is deeper and the facet is hollowed out along its length to form an elongate groove from the paraconid to the metaconid. The groove is worn more deeply on its lingual side than labially, so that the enamel on the labial side of the groove is higher than lingually (figs. 2B,C, 3B,C). In V 7482, wear has hollowed out the apex of the paraconid, but the paracristid is unworn. However, the posterolingual side of the protoconid and metaconid are deeply hollowed out along a continuous groove (figs. 2E–F). The pattern of apical wear in m1 implies a crushing action against the occluding teeth (ultimate upper premolar and M1) like that already seen in the premolars. The second wear pattern in m1, seen only in the holotype, is suggestive of vertical or near-vertical shear: The enamel on the labial side of the crown has been worn to form a facet that extends from the paraconid posteriorly to the upper parts of the side of the protoconid. The anteriormost parts of this facet have ventrally notched the anterior basal cingulid; another facet extends on the labial side from the protoconid to the metaconid (arrows on m1 of fig. 4A). Faint, steeply oriented parallel striae on these surfaces from contact with the occluding teeth imply elevation and slight retraction of the mandible during closure of the lower jaw.

The second, third, and fourth molars of the holotype of *Heishanlestes changi* can be characterized as spalacotheriid-like in coronal morphology: The crowns are anteroposteriorly compressed such that the trigonid angle is acute, and the angle becomes more acute from m2 to m4 (fig. 4). The protoconid is positioned slightly posterior to the mid-length of the crown, so that the anterior side of the trigonid is longer than the posterior side, which is more nearly transverse to the anteroposterior axis of the tooth row; hence, the triangle that the trigonid forms is slightly asymmetrical in occlusal outline. The protocristid is substantially higher than the paracristid on these teeth, as on m1, and probably was so before wear. Collectively, the mor-

phology of m2–4 contrasts markedly with that of m1, but there is much less difference from m2 to m4, which form an evenly graded series. Each of these three molars has three trigonid cusps. Although now worn, it is evident that the cusps originally increased in height on each tooth in the sequence of the paraconid–metaconid–protoconid. The paracristid is lower than the protocristid. The protoconid of m3 is taller than that on m4 (this cusp on both teeth appears to be unworn). The protoconid of m2 is deeply worn and its original height relative to the corresponding cusp on m3–4 cannot be determined, although by comparison with unworn lower molars of spalacotheriids, it was probably lower than that on m3. The base of the crowns is encircled by a robust cingulid. This cingulid is continuous across the labial side of the protoconid, where it is dorsally flexed. The height of the flexure decreases from m2 to m4, and the flexure on m2 is less than that on m1. On the lingual side of the crown, the cingulid is shallow and flexed dorsally between the base of the paraconid and metaconid, but with little difference in degree of flexure among the three teeth.

The interlock between successive molars from m1 to m4 is tightly constructed and is identical between teeth in this series (fig. 4B). Using the interlock between m2 and m3 as an example, the basal cingulid at the anterolingual corner of m3 projects anteriorly as a spurlike structure (mesial cingular cusp) that partly overlaps the spurlike posterolingual extremity of the posterior cingulid (distal cingular cusp) on m2. The posterior cingulid spur on the lower molars of *Heishanlestes changi* is probably homologous to the hypoconulid in other early mammals (e.g., *Kuehneotherium*; see Crompton, 1971: fig. 7A; Cassiliano and Clemens, 1979: fig. 7–2, cusp d in the terminology of Crompton and Jenkins, 1968), although a distinct elevated cusp or cusplule is hardly visible here in V 7480. The anterolingual spur is the most prominent anterior feature in the interlock between successive molars in V 7480. Its lingual projection agrees with the position of mesial cingular cusp in *Kuehneotherium* and *Morganucodon* (cusp e in the terminology of Crompton and Jenkins, 1968). There is no cusp f as seen in *Kuehneotherium* or *Tinodon*

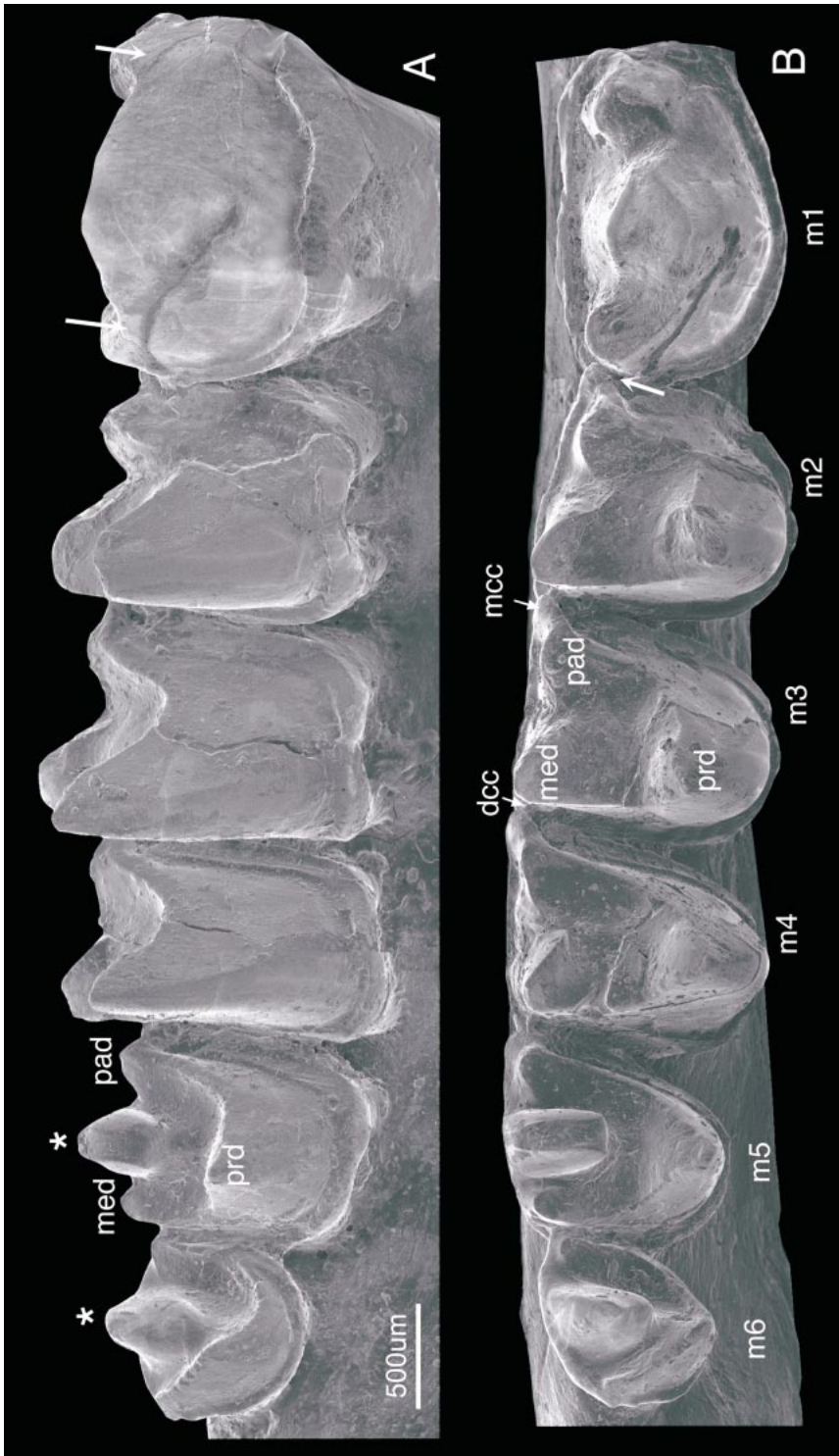


Fig. 4. SEM images of lower molars of *Heishanlestes changi* (cast of IVPP V 7480). **A**, lateral view; **B**, crown view. prd, protoconid; pad, paraconid; med, metaconid; dcc, distal cingular cusp; mcc, mesial cingular cusp; m1–m6, molars; *, large cusp in the middle of trigonid; arrows indicate anterior and posterior wear facets on m1.

(Crompton and Jenkins, 1968; Cassiliano and Clemens, 1979).

In V 7480, m2–4 are moderately worn over much of the occlusal surface of the trigonid, but wear decreases from m2 to m4. On m2, a continuous worn area extends over the lingual face of the protoconid (which is also chipped in this tooth), all of the protoconid, and the labial face of the metaconid, and continues anteroventrally to the base of the paraconid. Most of the paraconid has been worn away and the paracristid is deeply notched, as well; dentine is exposed through nearly the entire extent of this area. The m3 and m4 show the same pattern, although the lingual face of the protoconid on these teeth is less worn than on m2. Additionally, a well-developed vertical facet containing steeply angled parallel striae is evident over much of the anterior face (prevallid) on m2–4 (see fig. 4A). On the posterior face (postvallid), similar striae but no distinct facets are developed. These patterns suggest deep interembrasure prevallid–postvallum shear with the upper molars. By comparison, an emphasis on prevallum–postvallid shear is probably primitive among therians (Crompton, 1971). The cingulids between adjacent teeth abut along their length to form a gutter, which is worn as well.

The m5–6 comprise the third pattern of molar coronal morphology in V 7480 (figs. 1, 4). These two teeth are smaller and much lower than the more anterior molars, and m6 is considerably smaller than m5. In occlusal outline, the crown of m5 is triangular (although the trigonid angle, while still acute at about 50°, is more obtuse than in m4). The protoconid, which is better developed on m5 than on m6, is markedly lower than on the more anterior molars. The paraconid and metaconid are little developed. On m5, the paraconid is slightly elevated lingually. The metaconid is similarly constructed, but is smaller and lower than the paraconid. The paracristid and protocristid are unworn and are subequal in height. Between the paraconid and metaconid is an enlarged, erect cusp. It is labiolingually wider than anteroposteriorly long, arises abruptly from the lingual half of the occlusal surface and is the tallest structure on the crown (* in fig. 4A). This cusp appears to be a neomorph that is present

neither, even incipiently, on the more anterior molars nor on the molars in other known symmetrodonts. The neomorphic cusp is worn along its summit and down on to its labial face, in contrast to the paraconid, metaconid, and protoconid, which are unworn. The basal cingulid encircles the crown, except lingually, where it is absent. It is worn anteriorly, along its labiolingual extent with the posterior cingulid of m4. The interlock between m5 and m4 is like that between the more anterior molars, although cingular cusps here are weaker and, hence, the interlock more shallow.

The ultimate molar, m6, is the smallest of the series and probably would not be recognized as being from a symmetrodont if found in isolation. Its coronal outline is subcircular, longer than wide, and the labial face of the protoconid is broadly rounded, not angular. Its labial sides are oriented at about 60° from one another. As in m5, the occlusal surface is dominated by the central lingual cusp, which forms an anteroposteriorly compressed blade and is the tallest structure on the crown. The tip of this blade is worn, the only wear that this tooth displays. The paraconid and paracristid are developed as a broad planar shelf that continues labially to the protoconid, which is little elevated. The posterolingual corner of the crown, occupied by the metaconid on m1–5, supports a raised ridge (metaconid + protocristid) that joins the protoconid labially. This ridge is higher than the paraconid + paracristid, and is cuspidate along its summit, but the metaconid is reduced. The basal cingulid is reduced: it is narrow anteriorly, discontinuous across the labial face of the protoconid, and restricted to the base of the protoconid posteriorly. The mesial cingular cusp is weak. In spite of its small size, m6 is two-rooted.

DENTARY: The dentary of the holotype of *Heishanlestes changi* is nearly completely preserved; in V 7481 only the parts of the bone from the level of the canine to m1 are preserved, while in V 7482 the dentary from anterior to p3 to beneath m1 remains; together, these specimens present a rare opportunity to examine the structure in symmetrodonts of this important element (figs. 1–3, 5). As noted above, the anteriormost parts of the dentary are missing from all three specimens,

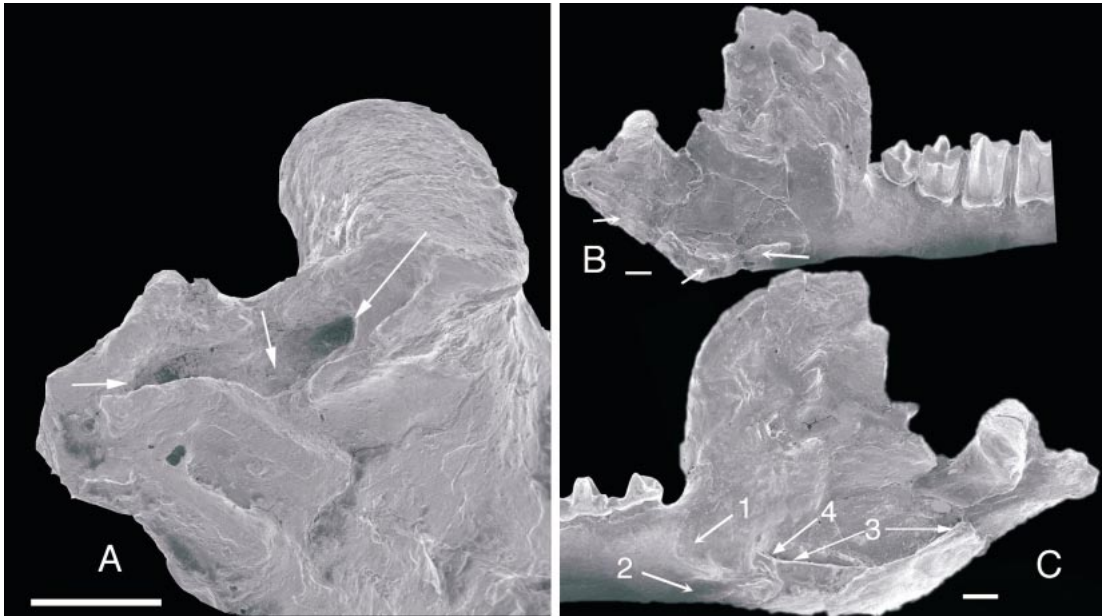


Fig. 5. SEM images of the right dentary of *Heishanlestes changi* (cast of IVPP V 7480). **A**, lateral view of the condylar process and the adjacent area; **B**, lateral view of the posterior part of the dentary; **C**, medial view of the posterior part of the dentary. Arrows in **A** indicate the small sulcus; arrows in **B** indicate the edge of the masseteric shelf; arrow 1, small depression at the root of the coronoid process; arrow 2, the depression anteroventral to the mandibular foramen; arrows 3, edge of the pterygoid crest; arrow 4, position of the mandibular foramen. Scale bars are 500 μm .

however, with no remnant of large incisor alveoli preserved.

The dentary is delicately constructed, in keeping with its small size (see measurements in table 1). The horizontal ramus is long, slender, and dorsoventrally shallow. Its ventral margin is nearly straight, rising only slightly anteriorly, beneath the anterior premolars and canine, and posteriorly, near the base of the condylar process. Its alveolar margin is straight through nearly the entirety of the preserved length of the dentary, except posteriorly, where it rises beneath m5 and m6. Hence, the horizontal ramus of the dentary is deepest beneath the ultimate molar. Small mental foramina open labially below the canine, p2, and p3 (indicated by arrows in fig. 2A). Lingually, the mandibular symphysis is best preserved in the holotype, in which it is conspicuous, forming a long, dorsoventrally shallow boss that weakens posteriorly but nonetheless extends to beneath p4 (fig. 1C). There is no evidence of an elon-

gate Meckelian groove extending posterior to the symphysis, as seen in *Zhangheotherium* (Hu et al., 1997: fig. 2c).

The coronoid process is virtually complete on the holotype, although it was somewhat crushed during burial and preservation (figs. 1, 5). Of its borders, only the mid-part of the posterior border has been broken away, so that its overall dimensions and outline as preserved are original (see table 1 for measurements). The process is high, erect, and relatively long anteroposteriorly through much of its height. Its anterior border is nearly vertical, meeting the alveolar border of the dentary at a right angle. The anterior border turns posteriorly toward the dorsal border at about two-thirds the height of the process. The dorsal border is faintly convex dorsally, and joins the posterior border of the process at a nearly right angle. There is no extension of the tip of the coronoid process posteriorly to form a deep supracondylar notch. In side view, the posterior border is only shallowly

concave and is inclined slightly anteriorly relative to the anterior border. Ventrally, as the posterior border approaches the condylar process, it turns more posteriorly.

The masseteric fossa is deep, especially anteriorly, where it is limited by a raised rim, and ventrally, where its ventralmost extent appears to have been bordered by a distinct laterally projecting shelf, the masseteric shelf (fig. 1A; arrows in fig. 5B; Kermack et al., 1973). The original dimensions of this shelf are uncertain, however, owing to postmortem crushing of the bone in this area; it may be that its proportions have been enhanced by distortion of these surfaces during burial, especially posteriorly. Nonetheless, it seems clear that the anterior and ventral limits of the masseteric fossa were originally well defined and that the fossa was correspondingly deep.

On the holotype, the medial side of the coronoid process appears originally to have been relatively flat over much of its extent (figs. 1C, 5C). Although the bone here has been distorted by crushing and breakage, there is no evidence of a well-defined fossa for the insertion of the deeper parts of the external mandibular adductor musculature (i.e., deep masseter and temporalis muscles) that must have extended over this surface. Nevertheless, the anterodorsal edge of the process does form a low ridge elevated slightly above the topography of the adjacent surface. On the medial side of the dentary just anteroventral to the base of the coronoid process a small rugose subcircular depression is developed; this is bordered ventrally by a short, narrow ridge, which is broken posteriorly (arrow 1 in fig. 5C). The depression may be the scar of attachment of a separate coronoid bone, which would have been articulated and lost between the death and final burial of this individual. It is also possible that the depression resulted from postmortem deformation or it is the anterior extension of pterygoid fossa. A similarly positioned but better defined scar, possibly for the coronoid, occurs in *Zhangheotherium* (Hu et al., 1997). Beneath the ridge that defines the depression ventrally in V 7480 is another shallow depression (arrow 2 in fig. 5C), which is rugose and elongated and opens into the pterygoid fossa. This is prob-

ably not an artifact of preservation, but lacks the sulcus-like appearance of a Meckelian groove. This depression in V 7480 could be related to absorption of Meckel's cartilage during development (Meng et al., 2003).

Below the coronoid process, the medial aspect of V 7480 is dominated by the pterygoid fossa (figs. 1B,C, 5C). In this specimen, the fossa extends deeply into the dentary and is delimited both ventrally and medially by an elevated pterygoid crest (arrows 3 in fig. 5C; see Cifelli and Madsen, 1999, for discussion of this structure in symmetrodonts) that encloses the fossa as an elongate pocket that opens dorsomedially. The modification of the crest to form a wall that partly encloses the pterygoid fossa medially is not an artifact of preservation, in which an originally ventral crest had been crushed dorsolaterally into the fossa. The anterior extremity of the pterygoid crest is either broken in V 7480 or it extends anterodorsally beneath the posterior edge of m6 if the depression there (arrow 1 in fig. 5C) is actually part of the fossa. In V 7480, the mandibular foramen probably opens within the anterior wall of the pterygoid fossa, but pieces of bone have been broken and displaced here, evidently covering the foramen and hiding it from view (arrow 4 in fig. 5C indicates the probable location of the foramen). As in other symmetrodonts, no angular process is developed ventrally below the pterygoid fossa, although the ventral margin of the dentary turns abruptly dorsally in a broadly obtuse angle, to join with the ventral margin of the condylar process. Perhaps the depressor mandibulae muscle inserted here. There is no evidence of a medially directed "pterygoid process" arising from the more anterior parts of the pterygoid crest, as in *Spalacolestes* (Cifelli and Madsen, 1999).

In V 7480, the condylar process extends strongly posterodorsally from the main body of the dentary (figs. 1, 5). It is bilaterally compressed and dorsoventrally deep, and it exhibits two unique features that appear not to be entirely artifacts of the postmortem damage that this part of the process has sustained. First, the process extends posterior to the condyle itself as a thin posterodorsally directed flange. This structure is in the position of a retroarticular process in more

primitive tetrapods, and we know of no counterpart of it in other mammals. Second, the flange is fissured along its dorsal edge, and this fissure (indicated by arrows in fig. 5A) extends anteriorly, on to the posterodorsal side of the condyle, laterally adjacent to its surface of articulation with the squamosal. Some degree of displacement of the condyle is evident, given that there is a crack between the condyle and its adjacent bone (best seen in medial view: fig. 5C). Therefore, the original size of the flange could have been smaller than as preserved. The flange is probably a supporting structure of the condyle rather than an angular process as seen in other mammals. The fissure itself is clearly not an artifact of preservation: Where visible, its interior surfaces are of smoothly finished bone. The fissure as preserved, moreover, appears to be somewhat narrower than in life, with much of its outer wall having been crushed into a central cavity.

The condyle itself is robustly constructed (figs. 1, 5). When the dentary is held horizontally, the articular surface of the condyle is located well dorsal to the tallest of the postcanine teeth and hence well above the alveolar margin of the dentary. The condyle is transversely expanded, more so medial to the plane of the condylar process than laterally. In V 7480, a low rim encloses the articular surface of the condyle, which is of unfinished bone and presumably was covered with thin cartilage in life (fig. 5A). Laterally, adjacent to the fissure, this surface faces mostly dorsally; medial to the plane of the condylar process, it continues down on to the posterior side of the condyle, suggesting the development of a postglenoid process of the squamosal.

COMPARISON AND DISCUSSION

Four tightly spaced premolars of *Heishanlestes* are unique among symmetrodonts, and have not been seen in other Mesozoic mammals. In marked difference from *Heishanlestes*, *Spalacotherium tricuspidens* has but three lower premolars, which follow one another successively along the tooth row, with no overlapping of the crowns (Simpson, 1928: fig. 19). In addition to the principal cusp, there is a posterior accessory cusp and

small anterior and posterior cingular cusps present on these teeth (Simpson, 1928: 100). Two lower premolars have been identified in *Zhangheotherium*: These are two-rooted, laterally compressed, have an anterior and posterior accessory cuspule, but lack a basal cingulid (Hu et al., 1998: 113). It has been suggested that *Maotherium* has three lower premolars (Ji, 2002; Rougier et al., 2003). They are probably similar to those of *Zhangheotherium* in crown structure. Articulated lower premolars are unknown in other spalacotheriids and while isolated lower premolars of spalacotheriids are undoubtedly present in collections, they are not readily sorted as to locus or assigned to species as known from lower molar dentitions (Cifelli and Madsen, 1999: 175). The worn areas on the tops of premolars of the new symmetrodont indicate a crushing function of these teeth. Premolars of some extant insectivores have flattened crowns, which can crush insect prey before shearing by the molars. The premolars of *Heishanlestes* may have functioned in a similar way.

Heishanlestes has six lower molars. *Zhangheotherium* also has six lower molars (Hu et al., 1997, 1998), *Symmetrodontoides canadensis* six or seven (Fox, 1976; Cifelli and Madsen, 1986, 1999), while both *Spalacotherium tricuspidens* and *Spalacolestes cretulablatta* have seven (Simpson, 1928; Cifelli and Madsen, 1999). Rougier et al. (2003) suggested that *Maotherium*, a close relative of *Zhangheotherium*, has six lower molars (note: Rougier et al. concluded that *Zhangheotherium* has only five lower molars, with which we do not agree). In all other symmetrodonts in which the molar series is known, the molars change gradually in size and morphology along the tooth row; none of them exhibits molar heterodonty resembling that in *Heishanlestes*. The m1, m2–4 and m5–6 of *Heishanlestes* form three morphologically discontinuous subsets of the molar family.

The first lower molar of *Heishanlestes changi* is strikingly similar to the tooth preserved in UALVP 12086 that was identified as m1 of *Symmetrodontoides canadensis* (Fox, 1972, 1976, 1985). As Cifelli and Madsen (1999: 177) discussed, UALVP 12086 may not pertain to *S. canadensis*, but

the resemblance of this tooth to m1 of *Heishanlestes changi* suggests it nonetheless may be an m1 of a symmetrodont, if not of *S. canadensis* then of one perhaps related to the Chinese species. Cifelli and Gordon (1999: 10) have illustrated similar teeth from the Upper Cretaceous of Utah as "Symmetrodonta, fam., gen., and sp. indet.", some of which may be m1 of this same group of symmetrodonts, as well. The worn area on the top of the m1 in *Heishanlestes* implies that m1 may have joined the premolars in crushing prey. On the other hand, the wear facets on the side of the crown indicate a shearing function of the tooth, which is more highly specialized in the middle teeth of the molar series. Therefore, in terms of function, m1 is transitional between premolar and molar series.

The m2–4 of *Heishanlestes* clearly exhibit characters of the Spalacotheriidae: The tooth crown is short and broad, the protoconid posteriorly located, and there is no talonid; the main cusps form an acute triangle; the distal cingular cusp is shifted to the posterolingual corner of the tooth; cusp f is not developed and the anterior cingulid, whether long or short, terminates lingually in the mesial cingular cusp; and posterior cingulid terminates lingually in the distal cingular cusp. All spalacotheriids show these same features. *Heishanlestes* has continuous prevallid and postvallid shearing surfaces, which are also seen in other spalacotheriids. In most spalacotheriids, the continuous shearing surfaces are present upon eruption, but in *Zhangheotherium* the surfaces are developed as a consequence of wear. *Maotherium* probably was similar to *Zhangheotherium* in these respects. The m2–4 of *Heishanlestes* have the paraconid and paracristid distinctly lower than the metaconid and protocristid, a feature also seen in the molars of North American spalacotheriids (Cifelli and Madsen, 1999: 206).

The m5–6 of *Heishanlestes* are smaller than the more anterior molars, a tendency also seen in other spalacotheriids. However, the large central cusp in these teeth is an interesting feature. Lower molars of late Triassic *Woutersia* also have a cusp (cusp g) lingual to the main cusp (cusp a of Sigogneau-Russell and Hahn, 1995). The genus was originally assigned to Symmetrodonta,

but probably related to Docodonta (Butler, 1997). The major cusps on these teeth (cusps a, b, and c in the terminology of Sigogneau-Russell and Hahn, 1995) do not form an elevated trigonid. Cone-shaped cusp g looks like an enlarged cingular cusp, similar to the large cingular cusp (cusp g) on the lower molars of *Morganucodon* (Crompton and Jenkins, 1968). Judged by morphology and location, cusp g of *Woutersia* and the central trigonid cusp on m5–6 of *Heishanlestes* are not homologous. The latter is the unique feature of *Heishanlestes*, with no homolog in other mammals. The wear facet on the top of the cusp suggests that it contacted the upper molars in occlusion, but its function is difficult to assess as the upper dentition of *Heishanlestes* is unknown. If upper molars of *Heishanlestes* were similar to those of other spalacotheriids, the neomorphic cusp on m5–6 might have occluded with cingulids or between the upper teeth.

Cifelli and Madsen (1999: 206) suggested that spalacotheriids have a unique interlocking mechanism between successive molars, with the distal cingular cusp lingual to the mesial cingular cusp of the next posterior tooth. However, this pattern is not present in *Heishanlestes changi* or between lower molars of *Symmetrodontoides canadensis*. Instead, in *H. changi* and *S. canadensis* (see UALVP 8588, holotype, right incomplete dentary with molars; Cifelli and Madsen, 1999: 177, discuss the identification of these teeth), the anterolingual corner of the basal cingulid slightly overlaps the posterolingual corner of the cingulid on the preceding molar. The cingular cusps become small spurs on both surfaces. Moreover, there is no embayment labial to the distal cingular cusp on the preceding tooth to accommodate the mesial cingular cusp in either *H. changi* or *S. canadensis*, nor does the overlap between the molar cingulids in these taxa really constitute an interlock at all. In *Zhangheotherium*, cingular cusps are well developed, but there is no interlocking mechanism between successive molars (Hu et al., 1998: 113).

The dentary of spalacotheriid symmetrodonts is very poorly known. The dentary of *Zhangheotherium* is virtually complete in the holotype; much of the gross morphology of the dentary of *Spalacotherium tricuspidentis*

can be reconstructed from separate specimens, although the bone surfaces are poorly preserved (see Simpson, 1928: fig. 19 and pl. 7). *Maothierium* is probably similar to *Zhangheotherium* in dentary morphology, but no detailed description is available (Ji, 2002; Rougier et al., 2003). In other known spalacotheriids, the dentary is represented only by fragments with teeth or has yet to be recovered (Fox, 1976; Cifelli and Madsen, 1986, 1999; Cifelli, 1990; Cifelli and Gordon, 1999). In *Spalacotherium* and *Zhangheotherium*, the symphyseal surface extends posteriorly only to beneath p1 (Simpson, 1928: fig. 19; Hu et al., 1997: fig. 2c). In *Heishanlestes*, the articulating surface of the symphysis is smooth, implying that during life the left and right dentaries were not fused and some independent movement between them was possible, a common feature in early mammals.

The broad and high coronoid process of *Heishanlestes* closely resembles those of spalacotheriids except *Zhangheotherium* and *Maothierium*. The coronoid process of *Zhangheotherium* is very differently constructed: It is slender, leans strongly posteriorly, and is pointed at its tip, which is well posterior to the base of the process (Hu et al., 1997: fig. 2c). The process in *Maothierium* looks similar to that in *Zhangheotherium* (Rougier et al., 2003). In the North American *Spalacolestes cretulablatta*, the anterior parts of the coronoid process are strongly flexed laterally (Cifelli and Madsen, 1999: 186), a modification not evident in *Heishanlestes*. The masseteric fossa is deep in *Heishanlestes* and delimited ventrally by a “flange-like” ventral masseteric shelf. The masseteric shelf is also seen in spalacotheriids in which the lower jaw is well preserved, as well as in *Gobiotheriodon*, a symmetrodont with broad-angle molars from Early Cretaceous of Mongolia (Averianov, 2002). *Shalbaatar*, a Cretaceous mammal based on an edentulous dentary, was reassigned as a spalacotheriid symmetrodont by Averianov and Archibald (2003). Its dentary also has a well-developed masseteric shelf. Since symmetrodonts lack an angular process on their dentaries, the masseteric shelf in some symmetrodonts probably helps expand the surfaces of attach-

ment for masseter muscles, implying larger muscles and greater biting power.

Heishanlestes lacks a distinct Meckelian groove along the medial side of its dentary. *Spalacotheroides* and *Spalacolestes* also lack this groove, although spalacotheriids other than those in Spalacolestinae, for example, *Zhangheotherium* and *Spalacotherium*, have a distinct Meckelian groove, as seen in many other Mesozoic mammals. The elevated pterygoid crest and pocket enclosed by the crest are well developed in *Heishanlestes* and *Spalacolestes* (Cifelli and Madsen, 1999); a similar but less developed condition is probably present in *Spalacotherium*, given the presence of an elevated pterygoid crest on the medial side of the dentary (Simpson, 1928: pl. VII; Cassiliano and Clemens, 1979: fig. 7–1). In *Zhangheotherium*, the crest is much less developed and does not enclose a pocket. A highly elevated pterygoid crest that encloses a pocket is not seen in mammals other than symmetrodonts. The pterygoid crest of spalacotheriids is probably for the insertion of a medial pterygoid muscle (Cifelli and Madsen, 1999: 173), and its hyperdevelopment with a pocket behind it in two spalacolestines may provide a more extensive surface for attachment of that muscle. In *Zhangheotherium*, the condyle, as preserved, is not so high as that of *Heishanlestes* although also higher than the alveolar margin of the dentary (Hu et al., 1997: fig. 2c). The articular surface of the dentary condyle in *Zhangheotherium* has not been described, but the glenoid cavity in that form is flat and anteroposteriorly elongate (Hu et al. 1997: fig. 3), suggesting that the condyle was not transversely expanded. The transversely expanded condyle of *Heishanlestes* is similar to those of soricomorph lipotyphlan insectivores. The supporting flange on the dentary of *Heishanlestes* has no comparable structure in other mammals, neither the fissure penetrating it nor the condyle. Heinrich (1998) reported a subcondylar groove on the dentary of a late Jurassic eupantothere, *Tendaguruthierium dietrichi*. But the groove is on the lingual side of the bone, extending from the condyle to the tip of the angular process. Heinrich interpreted that the groove probably supported angular bone. The fissure on the dentary of *Heishanlestes* probably did not

function as a site of attachment for posterior accessory bones of the lower jaw. If present, these bones would have been located on the medial, not the lateral, side of the dentary and hence, medial to the condyle. Although the flange and fissure do not appear to represent a teratological or other pathological deformity, we can suggest no function for them, nor are evident homologs known among other mammals.

Cifelli and Madsen (1999) founded a spalacotheriid subfamily, Spalacolestinae, for then-known North American Cretaceous spalacotheriids. The subfamily formed a monophyletic group in their phylogenetic tree (Cifelli and Madsen, 1999: fig. 19). The similarities between *Heishanlestes* and North American spalacolestines suggest a close relationship between them, while in terms of the morphology of m2–4, *Heishanlestes* is indeed more similar to *Spalacolestes* and *Symmetrodontoides* than is *Spalacotheroides* (Patterson, 1955, 1956; Cifelli and Madsen, 1999). From the coronal morphology of m2–4, the taxon may be deeply nested within North American genera, in which case the latter no longer form a monophyletic group.

If *Heishanlestes* is a spalacolestine, the occurrence of the subfamily in both North America and Asia indicates faunal connection/exchanges between two continents during the Early Cretaceous, a pattern that is paralleled by evidence from other fossil vertebrates (Cifelli et al., 1997). Averianov (2002) speculated that the survival of Spalacolestinae in North America is probably due to the rarity of eutherians in the medial Cretaceous there, and the invasion of the latter may have result in the rapid extinction of endemic Spalacolestinae in that continent, but the coexisting of *Heishanlestes* and eutherians in East Asia suggests that this is probably not the case. *Heishanlestes changi* has three types of lower molars and a flange supporting the condylar process, which, in turn, is penetrated by a sulcus. These features have never been seen before in mammals. A more satisfactory understanding of the function of these features and their role in helping *H. changi* survive in a competitive world must await the discovery of better preserved material than the holotype and referred specimens described in this paper. Nonetheless, it

seems clear that the rise of eutherians and marsupials may have eventually driven symmetrodonts, including those with the unusual specializations of *Heishanlestes*, to extinction.

ACKNOWLEDGMENTS

This project is supported by funds from the Chinese National Science Foundation (Grant # NSFC 40272010) and the Chinese Academy of Sciences (Grant # KZCX3-SW-127). YMH's research was also supported by fellowships from the University of Massachusetts, Amherst, and the American Museum of Natural History in New York, through the City University of New York. Jin Meng from the American Museum of Natural History kindly allowed YMH use of the facilities in his laboratory and provided invaluable suggestions to YMH's research. Approximately 50% of funds in support of RCF's continuing research on Cretaceous and Paleocene mammals is supplied by the Natural Sciences and Engineering Council of Canada; laboratory space for carrying out his research has been provided by the Department of Biological Sciences, University of Alberta. We are grateful to Shuhua Xie, Zhao Wang, Mingxin Dong, Wenhua Du, and Wei Gao from the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China, Zhenglu Chang from the Liaoning Technical University, Fuxin, China, and Takeshi Setoguchi from Kyoto University, Japan, who participated in the field work in 1994 and 1995. Shuhua Xie prepared the specimens. We thank G. Braybrook, University of Alberta, Canada, who took the SEM photographs, and D. Spivak, Royal Tyrrell Museum of Paleontology, Drumheller, Canada, for laboratory assistance.

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